Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change

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While the physical dimensions of climate change are now routinely assessed through multimodel intercomparisons, projected impacts on the global ocean ecosystem generally rely on individual models with a specific set of assumptions. To address these single-model limitations, we present standardized ensemble projections from six global marine ecosystem models forced with two Earth system models and four emission scenarios with and without fishing. We derive average biomass trends and associated uncertainties across the marine food web. Without fishing, mean global animal biomass decreased by 5% (±4% SD) under low emissions and 17% (±11% SD) under high emissions by 2100, with an average 5% decline for every 1 °C of warming. Projected biomass declines were primarily driven by increasing temperature and decreasing primary production, and were more pronounced at higher trophic levels, a process known as trophic amplification. Fishing did not substantially alter the effects of climate change. Considerable regional variation featured strong biomass increases at high latitudes and decreases at middle to low latitudes, with good model agreement on the direction of change but variable magnitude. Uncertainties due to variations in marine ecosystem and Earth system models were similar. Ensemble projections performed well compared with empirical data, emphasizing the benefits of multimodel inference to project future outcomes. Our results indicate that global ocean animal biomass consistently declines with climate change, and that these impacts are amplified at higher trophic levels. Next steps for model development include dynamic scenarios of fishing, cumulative human impacts, and the effects of management measures on future ocean biomass trends.

climate change impacts | marine food webs | global ecosystem modeling | model intercomparison | uncertainty

Climate change is altering the abundance and distribution of marine species (1–5), with consequences for ocean ecosystem structure and functioning, seafood supply, and marine management

Significance

Climate change can affect the distribution and abundance of marine life, with consequences for goods and services provided to people. Because different models can lead to divergent conclusions about marine futures, we present an integrated global ocean assessment of climate change impacts using an ensemble of multiple climate and ecosystem models. It reveals that global marine animal biomass will decline under all emission scenarios, driven by increasing temperature and decreasing primary production. Notably, climate change impacts are amplified at higher food web levels compared with phytoplankton. Our ensemble projections provide the most comprehensive outlook on potential climate-driven ecological changes in the global ocean to date and can inform adaptive management and conservation of marine resources under climate change.

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and conservation (6–8). Quantifying future trends and uncertainties is critical to inform ongoing global assessments (1), including the Intergovernmental Panel for Climate Change (IPCC) and Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, and guide viable pathways toward achieving key policy objectives, such as the United Nations Sustainable Development Goals (SDGs). Various modeling approaches exist to assess current and future impacts on marine ecosystems (8–12), yet each individual model is necessarily an incomplete simplification of the natural world, with different assumptions, structures, and processes (13). One approach to overcoming any single-model limitations is to force a suite of models with standardized climate change scenarios and combine them into ensemble projections to estimate mean future trends and associated intermodel spread (13). Such model intercomparison projects (MIPs) have become a "gold standard" in climate science and have proven critical for enhancing credibility and understanding of the physical and biochemical climate change projections (14) and associated impacts on Earth's terrestrial biosphere (15–17), yet can only now be attempted for the global ocean ecosystem (13).

Over the past decade, a number of global fisheries and marine ecosystem models (MEMs) have been developed (13). Some of these have been used individually to project future changes in species distribution, biomass, or potential fisheries catch (8–12), but it remains unclear how consistent and comparable these results are, and thus how applicable for providing robust insight and advice. The Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP; ref. 13) was created to bring these various models and modeling groups together to produce ensemble projections under standardized climate change scenarios.

Here we assess projected changes in global marine animal biomass over the 21st century through ensemble projections with six published global MEMs from Fish-MIP, forced with standardized outputs from two contrasting Earth system models (ESMs) and four emission scenarios [Representative Concentration Pathways (RCPs)]. The MEMs range from size-structured [Bioeconomic Marine Trophic Size-spectrum (BOATS), Macroecological] and trait-based [Dynamic Pelagic Benthic Model (DPBM), Apex Predators EcoSystem Model (APECOSM)] to species distribution [Dynamic Bioclimate Envelope Model (DBEM)] and trophodynamic models (EcoOcean) (*SI Appendix*, Tables S1 and S2). The ESMs span the range of available Coupled Model Intercomparison Project Phase 5 (CMIP5) projections, from low [Geophysical Fluid Dynamics Laboratory Climate Model (GFDL-ESM2M)] to high Institute Pierre Simon Laplace Climate Model (IPSL-CM5A-LR) increases in sea surface temperature (SST) and associated changes in net primary production (NPP), while other drivers were more similar (ref. 14 and *SI Appendix*, Figs. S1 and S2). The RCPs range from a low-emission strong mitigation scenario (RCP2.6) to a high-emission business-as-usual scenario (RCP8.5), with two intermediate scenarios (RCP4.5 and RCP6.0). All climate change scenarios were run for historical (1970–2005) and future (2006–2100) periods without fishing to isolate the climate signal, and with fishing to evaluate how climate responses differ in an ocean fished at current levels of intensity (13). The six MEMs generated standardized outputs of total animal biomass (except zooplankton) and biomass of animals of >10 cm and >30 cm. Since not all MEMs could run the full set of scenarios, due to MEM or ESM limitations, we analyzed all available runs for each scenario, and performed sensitivity analyses on subsets, which revealed similar results (*SI Appendix*, Table S3).

The goals of this study were to examine the consistency of projections across MEMs over a range of climate change scenarios globally and regionally from 1970 to 2100. We also evaluated how ocean animal biomass changes correspond with those in the physical environment and the extent to which projected climate impacts on primary producers and zooplankton (18) are transmitted to higher food web levels.

Results and Discussion

Ensemble Projections of Global Ocean Animal Biomass. Our ensemble projections revealed consistent declines in global marine animal biomass from 1970 to 2100 across all emission scenarios (RCPs, Fig. 1*A*). Almost all scenarios and MEM–ESM combinations predicted decreasing animal biomass (*SI Appendix*, Table S3), although the magnitude of decline varied among models. This general trend can be explained by warming causing increased ocean stratification, which reduces nutrient availability in the upper ocean, leading to decreased primary production and lower energy supply for higher trophic levels (14, 18), and changes in metabolic rates, among others (19). Without fishing, mean total biomass declines ranged from 4.8% (±3.5% SD) under low emissions (RCP2.6) to 17.2% (±10.7% SD) under high emissions (RCP8.5) by 2090–2099 relative to 1990–1999 (Fig. 1*A*). All four emission scenarios projected similar declines by 2030, the target year of many SDGs, and through to midcentury, after which they began to diverge. Projected mean biomass declines were similar for animals of >10 cm and >30 cm (Fig. 1*C*), albeit slightly lower and more variable for those of >30 cm (*SI Appendix*, Fig. S5 and Table S3). Thus, the consequences of different emission scenarios may not be distinguishable over the next two to three decades but differ markedly in the long term.

Climate Change Effects in a Fished and Unfished Ocean. Three MEMs were also able to run simulations with fishing, including time-varying historical and constant future fishing pressure (*SI Appendix, SI Methods*), which we used to compare projected climate change effects (RCP8.5 vs. RCP2.6) with and without fishing. The magnitude and variability of the climate change effect were similar (Fig. 1*D*), suggesting that fishing, at least under current levels of intensity, may not substantially alter the relative effect of climate change. The slightly weaker climate change effects with fishing (mean difference 2 to 3%; Fig. 1*D* and *SI Appendix*, Fig. S6*A*) may be due to an indirect effect: Warming enhances both growth and predation rates, yet predation rates are reduced due to selective fishing of larger animals and lower predator abundance (20, 21) which may indirectly enhance prey biomass and weaken the relative climate change effect (19). This is a relatively small effect, however, compared with the large direct effect of fishing itself, which resulted in 16 to 80% lower biomass for animals of >10 cm and 48 to 92% for animals of >30 cm compared with unfished conditions in 2100 under RCP2.6, and slightly lower values under RCP8.5. We note that the absolute magnitude of the fishing effect is not directly comparable across MEMs, due to inherent differences in how fishing pressure and commercial versus noncommercial taxa are incorporated (*SI Appendix, SI Methods*). We also caution that our future constant fishing scenario is simplistic and does not incorporate potential changes in effort, technology, management, and conservation (11, 21–23), which are likely to strongly affect future biomass trends. Nevertheless, a possible consistent climate change effect is an important consideration in the context of marine management and conservation.

Variability among Model Projections. Although ensemble means revealed global biomass declines across all emission scenarios (Fig. 1*A*), there was considerable variation among MEMs and ESMs (Fig. 1*B*). The latter largely reflects differences in SST increases and NPP reductions among ESMs (*SI Appendix*, Fig. S1), in addition to other physical and biochemical drivers (14), and reinforces previous work highlighting the importance of ESM and scenario uncertainty in future projections of fish biomass or fisheries production (24, 25). Interestingly, the variability in projected biomass changes among ESMs was of similar magnitude to that among MEMs (Fig. 1*E*), suggesting similar levels of uncertainty associated with physical and biological models. Since the field of global ecosystem modeling is relatively new compared with Earth system modeling (13, 14), one might have expected higher variability across MEMs. Other MIPs also found that uncertainties in both ESMs and climate impact models contribute to overall projection
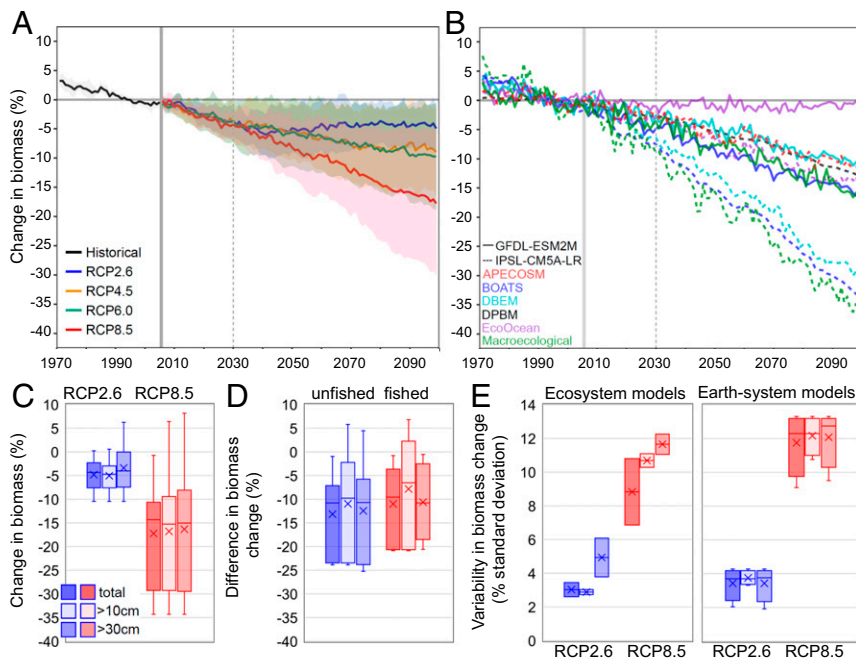
Fig. 1. Ensemble projections of global ocean animal biomass with climate change. (*A*) Multimodel mean change in total biomass without fishing for historical and four future emission scenarios (RCPs) relative to 1990–1999 with 1 SD (±SD, *n* = 10); thin vertical line indicates target year for achieving SDGs. (*B*) Individual model projections for RCP8.5 without fishing showing the spread across different ecosystem model and ESM combinations. (*C*) Projected biomass declines for three size groups in 2090–2099 relative to 1990–1999 under low (RCP2.6) and high (RCP8.5) emissions without fishing (*n* = 10). (*D*) Projected climate change effect (RCP8.5 vs. RCP2.6) in 2090–2099 for three size groups with and without fishing (*n* = 6). (*E*) Variability in biomass projections (expressed as SD of % change) due to different ESMs and different MEMs under RCP2.6 and RCP8.5 without fishing for three size groups (*n* = 10). Box plots display the median (horizontal line), mean (x), and interquartile range (boxes).

uncertainty, with similar contributions from ESMs and global hydrological models (15), yet much higher uncertainty in global crop and vegetation models than ESMs (16, 17).

The variability among MEMs can be attributed to differences in fundamental structures, taxonomic groups, and ecological processes. Generally, some MEMs respond strongly to temperature changes affecting metabolic rates (BOATS, Macroecological), while others are strongly driven by NPP changes affecting trophic dynamics (EcoOcean), or a combination of temperature, NPP, and additional drivers (e.g., pH, oxygen, ice cover) affecting habitat niches and species distribution (DBEM) or food web dynamics (DPBM, APECOSM) (13, 26). The MEMs also differ in whether species interactions (e.g., predation, competition), movement, or dispersal is included (*SI Appendix*, Table S1), which can alter their response and result in compensatory changes (27, 28). Some MEMs also allow for adaptive responses of species or communities to changing environments (e.g., size-structured and species distribution models), while others do not. Notably, the variability of projected changes among both MEMs and ESMs was higher under RCP8.5 than RCP2.6 (Fig. 1*E*), and the variability among MEMs was higher in animals of >30 cm than other size groups, suggesting greater projection uncertainty with stronger warming and for larger animals.

Empirical Validation. All MEMs included in this study have been individually tested across a range of physical and biogeochemical variables, and outputs have been compared with empirical data across multiple temporal and spatial scales (*SI Appendix, SI Methods* and Fig. S3). In addition, we compared our ensemble projections against biomass trends of scientifically assessed fish stocks representing 25 to 33% of the global fisheries catch (29, 30). First, we extracted results of a recent analysis (30) hindcasting the effect of warming on the maximum sustainable biomass yield (MSY) of 235 assessed fish populations globally in the absence of fishing (Fig. 2). Temporal trends matched those of our ensemble projections without fishing (*n* = 10 MEM–ESM combinations), and correlations suggest a good fit for the ensemble mean ($R^2 = 0.44$), which was higher than for most individual models ($0.13 \leq R^2 \leq 0.47$), reflecting the strength of the ensemble approach. We also compared biomass projections with fishing (*n* = 6 MEM–ESMs) to average biomass relative to biomass at MSY (B/B_{MSY}) across 331 assessed and exploited fish stocks (ref. 29 and *SI Appendix*, Fig. S4). Again,

temporal trends and correlations for the ensemble mean showed a better fit ($R^2 = 0.96$) than individual models ($0.80 \leq R^2 \leq 0.94$). These analyses suggest that our ensemble projections reflect observed trends for assessed fish stocks, providing confidence in our historical and future projections.

Trophic Amplification of Marine Biomass Declines. Although we did not find major differences in biomass changes among our three size groups (Fig. 1*C*), the combined biomass of higher trophic levels from our MEMs declined more strongly than that of lower trophic levels from ESMs across all RCP scenarios (Fig. 3). This trophic amplification of biomass declines has been previously shown for phytoplankton and zooplankton across a range of ESMs (18), and our results suggest this effect may extend to higher food web levels. Such amplification of the climate signal from primary producers to higher trophic levels arises from multiple factors that vary among ESMs and MEMs, including changes in phytoplankton size composition, lengthening of food chains, reduced trophic efficiencies, and higher metabolic costs with increased body size (18). In addition to larger mean biomass declines, we also observed larger variability for higher trophic levels, particularly at higher RCPs (Fig. 3). Mean NPP, phytoplankton, and zooplankton declines and variability from our two ESMs were comparable to those of other ESM ensembles (14, 18). We caution that many MEMs only use NPP or phytoplankton biomass as forcing variables directly influencing higher trophic levels (*SI Appendix*, Table S2), and cannot resolve all underlying food web mechanisms. Nevertheless, the consistency of the response across diverse ESMs and MEMs does suggest a general pattern of higher trophic levels being more likely to show larger biomass declines than lower trophic levels. This raises concerns about wider impacts of climate change on the structure, function, and stability of ocean ecosystems (31, 32), especially in combination with other human stressors, such as fishing, that disproportionally affect higher trophic levels, a process called trophic downgrading (33).

Trends in Relation to Global Temperature Changes. Many policy processes use the change in global air temperature since preindustrial times as a reference for the effects of climate change (34, 35). For our ensemble projections, this revealed a consistent linear relationship with an average 5% drop in total animal biomass with every 1 °C of Earth surface warming in the absence of fishing
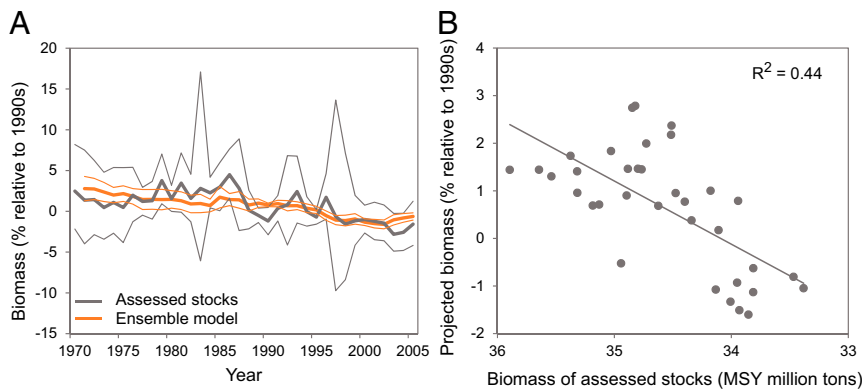
Fig. 2. Empirical validation of ensemble projections. Shown is the relative biomass change (animals of >10 cm) for our multimodel mean without fishing (orange line, ±95% CI, $n = 10$) compared with temperature-dependent hindcasts of MSY for 235 assessed fish stocks that are independent of fishing effects (gray lines, ±95% CI; ref. 30). Both projected and empirical biomass trends are displayed as (*A*) time series and (*B*) yearly scatter plot with a linear regression fit. A similar analysis of biomass trends with fishing is shown in *SI Appendix*, Fig. S4.

(Fig. 4). Similar declines were found for animals of >10 cm and >30 cm (*SI Appendix*, Fig. S7). These relationships may be slightly less negative in a fished ocean, given the dampening effect described above, yet overall biomass reductions remain substantial (i.e., 15% instead of 17% decline under highest warming; *SI Appendix*, Fig. S6B). Individual ecosystems may well show more complex responses to warming (3, 36), but these simple relationships represent well-founded approximations for a global average response. Recent results hindcasting temperature effects on biomass of 235 assessed fish stocks found a 4.1% drop in MSY from 1930 to 2010, a period that saw an average 0.6 °C of warming (30). This reconstructed rate of change is consistent with our 5% drop in biomass per 1 °C of warming throughout the 21st century. According to these results, limiting future warming to 1.5 °C to 2.0 °C above preindustrial levels would limit biomass declines to 4 to 6% by 2100, underscoring the potential impact of climate change mitigation according with the Paris Agreement (34, 35).

Spatial Patterns of Biomass Change. Not all ocean regions respond similarly to climate warming (Fig. 5 and *SI Appendix*, Fig. S8). Our ensemble projections revealed strong increases in total animal biomass in polar regions and widespread declines in temperate to tropical regions under RCP8.5 (Fig. 5*B*), with qualitatively similar but less pronounced patterns under RCP2.6 (Fig. 5*A*). The climate change effects were spatially similar with and without fishing (*SI Appendix*, Fig. S9). However, our ensemble projections differed spatially from previous single-model results highlighted in the IPCC's Fifth Assessment Report (1): We found strong biomass declines (not increases) in many temperate to subtropical regions and increases (not declines) around Antarctica. The magnitude of regional changes also varied from other single-model results (8–11). Generally, warming waters and enhanced primary production are expected to facilitate species expansions and biomass increases in polar regions, while tropical areas may experience pronounced species losses as thermal thresholds are exceeded. In temperate regions, warming is expected to change species composition, and reduced primary production due to enhanced stratification will result in biomass declines (3, 4, 30). Our ensemble projections showed high model agreement on the direction of change in many ocean regions (75 to 100%; Fig. 5 *E* and *F*), providing confidence in our multimodel results that combine different ecosystem structures and processes. Many models also agreed relatively well on the magnitude of projected changes in temperate to tropical regions but showed considerable intermodel variability in many polar and coastal regions (Fig. 5 *C* and *D*), reflecting differences among ESMs and MEMs (*SI Appendix*, Figs. S10 and S11). These results again underscore the importance of model intercomparison in identifying uncertainties and constraining expected outcomes of ecosystem changes in the ocean.

Conclusions

Our ensemble projections demonstrate that global ocean animal biomass consistently declines with climate change, and that impacts are amplified at higher trophic levels. Our hindcasts support recent empirical work that shows ongoing climate impacts on fish biomass (30, 37), and project elevated climate-driven declines in ocean ecosystems, with magnitudes dependent on emission pathways. Amplification of biomass declines for higher trophic levels represents a particular challenge for human society, including meeting the SDGs for food security (SDG2), livelihoods (SDG1), and well-being (SDG3) for a growing human population while also sustaining life below water (SDG14). Our ensemble projections indicate the largest decreases in animal biomass at middle to low latitudes, where many nations depend on seafood and fisheries, and where marine biodiversity is already threatened by multiple human activities (6, 38). In turn, the largest increases are projected at high latitudes, highlighting new opportunities for—and potential conflict over—resource use, but also an urgent need for protecting sensitive species and rapidly changing ecosystems. Overall, our results clearly highlight the benefits to be gained from climate change mitigation, as all impacts were substantially reduced under
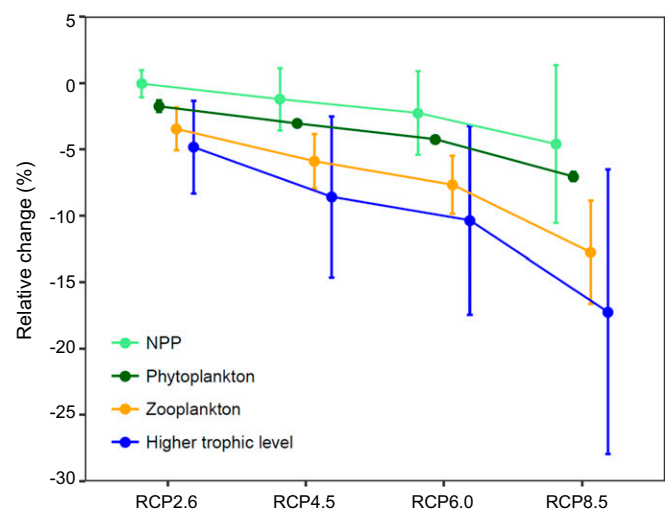
Fig. 3. Trophic amplification of marine biomass declines. Shown is the magnitude of projected mean changes in 2090–2099 relative to 1990–1999 (percent, ±SD) for NPP, phytoplankton, and zooplankton biomass derived from ESMs ($n = 2$) and higher trophic levels from MEMs across four RCPs ($n = 10$ for RCP2.6 and RCP8.5; $n = 8$ for RCP4.5 and RCP6.0). All ecosystem models use either NPP or phytoplankton biomass as forcing variables, and some also use zooplankton biomass.

Fig. 4. Projected biomass trends in relation to global air temperature changes. Shown is the relationship of the change in marine animal biomass to increasing global surface air temperature since preindustrial times (1860s). Each dot represents an annual ensemble mean (*n* = 10) relative to 1990–1999 across historical and future emission scenarios (RCPs) in the absence of fishing. Vertical lines frame expected changes between 1.5 °C and 2 °C of warming.

a strong mitigation (RCP2.6) compared with the business-as-usual (RCP8.5) scenario.

By providing estimates of global biomass changes and associated uncertainties, our ensemble projections represent the most comprehensive outlook on the future of marine animal biomass to date. Our results are robust in terms of the direction of change, yet the substantial spread in the magnitude of projections illustrates considerable uncertainty in both ESMs and MEMs. The challenge

is to address these uncertainties and improve our ability to predict marine ecosystem responses to climate change at different temporal and spatial scales. Projections based on global models are often less certain for coastal and polar regions but may be improved through regional downscaling to incorporate higher-resolution climate and ecosystem features (7, 39). The next round of CMIP6 projections with improved representation of biochemical parameters may also advance future ensemble projections (13, 40). The expansion of global observational datasets provides further opportunities to better constrain and validate models. The incorporation of additional MEMs based on novel paradigms or reflecting alternative structures and processes may also be informative (13), along with regional ecosystem or fish stock models that more accurately capture processes at management-relevant scales (21, 41, 42). Future MEMs could also further explore how species interactions and potential acclimatization or adaptation of marine organisms modify projected distribution and abundance.

Finally, a large component of future change will depend on the trajectories of fisheries, aquaculture, and other human impacts on the ocean (6, 11, 29, 38). Incorporating standardized temporally and spatially resolved scenarios of human activities and alternative management approaches will improve our understanding of the future of marine animals and ocean ecosystems (13, 23), and identify the points of greatest leverage for mitigating impacts. Improved dynamic and adaptive ecosystem-based management may mitigate some future climate change impacts and maintain ecosystem health and service provision (6, 21, 22, 43). However, this can only happen if the international community, including national and regional bodies, strengthens the required institutions and management approaches (6, 44).

Methods

Model Selection. The six global MEMs varied in their model structure, processes, representation of functional groups, size classes or commercial taxa, and how they incorporated ESM-derived climate forcings and fishing (*SI Appendix, SI Methods* and Tables S1 and S2). Our ensemble thus includes a greater variety of ecosystems components and processes than any single model.

Fig. 5. Spatial patterns of projected biomass changes. Shown are global ensemble projections at a 1 × 1 degree resolution for (*A, C,* and *E*) RCP2.6 and (*B, D,* and *F*) RCP8.5. (*A* and *B*) Multimodel mean change (percent, *n* = 10) in total marine animal biomass in 2090–2099 relative to 1990–1999 without fishing. (*C* and *D*) Variability among different ecosystem model and ESM combinations expressed as 1 SD. (*E* and *F*) Model agreement (percent) on the direction of change.

Climate Change Scenarios. The two ESMs from CMIP5 (https://pcmdi.llnl.gov/?cmip5/) provided the necessary physical and biochemical outputs to force our MEMs, particularly monthly depth-resolved fields of phytoplankton and zooplankton size groups (*SI Appendix*, *SI Methods* and Table S2). Average trends of GFDL-ESM2M and IPSL-CM5A-LR reflect the multimodel mean and range of a broad set of CMIP5 models (14). The four RCPs represent standard IPCC informed emission scenarios (*SI Appendix*, *SI Methods*).

Simulations. All MEMs ran simulations without fishing, and three MEMs ran simulations with fishing for historical (1970–2005) and future (2006–2100) periods. Historical fishing reflected time-varying effort or mortality rates depending on MEM requirements, and future fishing was kept constant at 2005 levels (*SI Appendix, SI Methods*). Not all MEMs performed all simulations, and sensitivity analyses cross-checked subsets of results (*SI Appendix*, Table S3).

Analyses and Validation. Annual outputs of total animal biomass density (grams carbon per square meter) and animal biomass of >10 cm and >30 cm were derived on a 1 × 1 degree grid. We calculated time series of % biomass change from 1970 to 2100 relative to 1990–1999 (reference period), and % biomass change in 2090–2099 vs. 1990–1999 for each simulation, as absolute biomass densities were not strictly comparable across MEMs. Relative changes were combined into ensemble means and SD. The climate change effect [(RCP8.5 − RCP2.6)/RCP2.6] was calculated in a fished and unfished ocean within and across MEMs. Empirical validation was achieved by comparing historical projections with biomass trends of assessed fish stocks in a fished ocean (B/B$_{MSY}$; ref. 29) and temperature-dependent biomass hindcasts (MSY) of assessed stocks without fishing (30), in addition to published individual MEM validations with empirical data (*SI Appendix*, Fig. S3). Trophic amplification was evaluated by comparing mean (±SD) changes (2090s vs. 1990s) in NPP and total phytoplankton and zooplankton biomass from ESMs

with higher trophic level biomass from MEMs across RCPs. Mean biomass changes were also compared with global air temperature changes since preindustrial times (1861–1870) from ESMs. Spatial patterns were mapped as mean % biomass changes in 2090–2099 vs. 1990–1999, the SD of the mean to assess intermodel variability in the magnitude of change, and the % model agreement on the direction of change (14). We also mapped the climate change effect with and without fishing and the variability of results across ESMs and MEMs. For further details, see *SI Appendix, SI Methods*.

Data Accessibility. All data reported in this paper are archived (45) and publicly available at http://dataservices.gfz-potsdam.de/pik/showshort.php?id=escidoc:2956913.

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